Observations on the Life-histories of Gamasinæ, with a view to assist in more exact Classification. By Albert D. Michael, F.L.S., F.R.M.S.

[Read February 3, 1881.]

(PLATES XXII. & XXIII.)

My intention in this paper is to record the results of a series of observations, made during the year 1880, upon the life-histories of a few species of Gamasinæ, with the special object of endeavouring to decide some of the disputed points in reference to these creatures, which render any thing like knowledge of the family so difficult.

It will readily be understood how these difficulties arise on the very threshold, when the two gentlemen who have probably paid more attention to the subject than any one else living, viz. M. Mégnin of Versailles and Dr. Kramer of Schleusingen, are totally at variance upon such primary matters as whether certain conspicuous characteristics are fixed distinctions, affording a good basis for subgeneric and specific division, or whether they are simply marks of an immature stage, which will vanish upon attaining maturity.

During my late researches into the life-histories of another family of Acarina (the Oribatidæ), the results of which are recorded elsewhere*, I have become strongly impressed with the idea that detached observations, on captured specimens, are of secondary value, and that really reliable information upon the subject is only to be obtained by breeding the creatures in confinement, in vessels known not to contain any allied Acarina, and which will afford the means of very frequent observation of the individual specimens which are being traced. Great care and attention, however, is required to keep the creatures alive and healthy under these conditions. It is easy to breed numbers in large vessels containing quantities of shelter and food; but these are of comparatively little service, as the individual specimen is lost sight of.

It seemed to me that if some of the Gamasids could be bred through their lives, and watched in this manner, several of the questions above alluded to might be set at rest; but for a long

^{*} Journal of the Royal Microscopical Society, vol. iii. p. 32.

time I was not as successful in rearing the Gamasinæ as I had been with the Oribatidæ. The former are far more active creatures, and did not thrive when confined in the small glass cells which I had used for the latter, and which are so handy for observations. I have at last succeeded in keeping the several species which I have attempted in good condition, and rearing them several generations, by using very large cells, and small round glass dissecting-troughs, each being covered by a flat plate of glass with two or three small holes in it, each hole being covered with very fine muslin gummed outside the glass, the cover being larger than the cell, and the holes in such a position that they can either be made to come over the interior of the cell so as to ventilate it, and allow the escape of moisture, or pushed beyond the cellwall leaving the moisture confined. This arrangement, combined with a curtain, and, what is more important, care and frequent attention, enabled me to regulate the light, temperature, and hygrometric condition of the air in the cell, so as to obtain in each instance what was most suitable to my captives. They finally became apparently quite at home and contented in their prisons, not attempting to escape when the cell was sometimes uncovered for the use of higher powers: this is a great point, because habits cannot be observed when the creatures are excited and endeavouring to escape.

One very doubtful point had to be decided at the outset, viz. what the Gamasinæ really fed upon, as they manifestly could not be successfully reared unless supplied with proper food. Mégnin says* they are nourished on the liquid products of the decomposition of dead vegetables or the excrements of quadrupeds and birds; and he proceeds to cite the places where they are found as proof of this assertion. He is also decidedly of opinion † that the nymphs and females do not obtain any nourishment from the insects upon which they are so constantly found, but simply use them as a means of conveyance. Kramer also states‡ that damp and decaying vegetation are the necessaries of their existence. I did not find, however, that the Gamasids which I attempted to

^{* &}quot;Mémoire sur l'organisation et la distribution zoologique des Acariens de la famille des Gamasides," Robin's Journ. de l'Anatomie et de la Physiologie, May 1876, p. 325.

[†] Loc. cit. p. 290.

^{‡ &}quot;Zur Naturgeschichte einiger Gattungen aus der Familie der Gamasiden," Archiv für Naturgeschichte, 1876, erstes Heft, p. 47.

rear throve at all well when supplied only with decaying vegetation; and a comparison of their construction with that of other families of Acarina led me irresistibly to the conclusion that they were chiefly or entirely predatory. The remarkable power of darting each mandible separately with speed and accuracy of aim far in advance of the body, the powerful retractile muscles attached to these mandibles, the organization of the remainder of the mouth, the extreme swiftness of the creatures, the use of the front legs as tactile organs only, and not for the purposes of locomotion, and the ample supply of tactile hairs in front only all seemed to me to fit the animals for a predatory life, and to indicate habits similar to those of Cheyletus and Trombidium rather than of the true vegetable-feeders, such as the Oribatidæ, Tetranachi, &c. In this I was confirmed by frequently capturing Gamasids with small Thysanuridæ firmly held in their mandibles, a circumstance surprising enough, as one would hardly have expected that any development of the tactile sense would have enabled an eyeless being such as Gamasus to capture such active insects as Podura &c.; they are, however, certainly able to do so.

There are one or two remarks in the earlier writers which point in the direction of predatory habits. Thus Dugès*, speaking of the so-called Gamasus coleoptratorum, says :- In winter they are found under stones, and there doubtless live on other Acari; at all events, I have seen small Trombidies devoured by Gamasus testudinarius. Gervais also †, speaking of an unidentified species, says:-I have seen it seize a small Myriapod in its didactyle mandibles and run off rapidly with it. Led by these considerations, I determined to try feeding my Gamasids with cheesemites. I first placed a single Gamasid in a cell and shook in some cheese-mites; the success was quite unmistakable. The instant that a cheese-mite touched one of the tactile hairs on the fore legs of the Gamasus, it was seized in the mandibles of the latter. drawn to the mouth, and sucked dry; the same took place with another and another, until the Gamasus was satiated. Since that time I have fed my Gamasids entirely upon cheese-mites with complete success; but they have sometimes varied their diet by eating one another. I am therefore of opinion that, at all events

^{* &}quot;Recherches sur l'ordre des Acariens." Troisième mémoire. Ann. des Sci. Nat. 1834, t. ii. p. 26.

[†] Walckenaer's 'Histoire naturelle des Insects, Aptères,' t. iii. p. 215.

as a rule, the Gamasinæ are predatory creatures, and that their being found in the situations before described is due to the fact that soft-bodied *Acari*, and minute soft-bodied insects &c., abound there, and afford ample prey.

While on this subject of the food, I wished, if possible, to ascertain whether the nymphs and females of Gamasinæ do really suck the juices of the insects upon which they are found, or only use them as a means of conveyance, as Mégnin contends. With this object, I placed a single Gamasid in a separate cell, and after a day or so ceased feeding it with a very sufficient supply of cheesemites, but instead introduced some freshly killed dipterous insects, selecting those the juices of which would be dark or of strongly marked colour. The Gamasinæ, like many other of the Acarina, are sufficiently transparent to allow the colour of the food to show through the dorsal surface, looking like coloured markings; a circumstance which, not being understood by C. L. Koch*, induced that most laborious writer to create a great number of new species, dependent upon colour, which arose from the nature of the food the creature had been eating. I invariably found that for a day or so the Gamasus assumed the colour of the insect supplied to it. Thus after a black gnat had been put in, the markings on the Gamasus were black, after a scarlet Trombidium they were red; and I also observed that if the insect were at all large, the Gamasus seemed to prefer attacking the eye, and was then coloured for a day or so in accordance with the pigment-layer. It is therefore evident that the Gamasids do suck the juices of quite freshly killed insects; and although it is most difficult to watch them on the living insect, I cannot help thinking that they do obtain some amount of nourishment at the expense of their hosts during the period of their parasitism, or at all events that this is the case with some species.

Having now disposed of the question of food, I will relate the other observations which I was able to make; but before doing so, in order that the points I wished to elucidate may be understood, it is, I fear, necessary to show, very shortly, what other writers have done on the subject, and where the divergence of opinion principally exists.

Linnæus, who did not divide the Acari into families, found

^{* &#}x27;Deutschlands Crustaceen, Myriapoden und Arachniden' (Regensburg, 1839).

and named Acarus coleoptratorum*, which is found abundantly parasitic upon Coleoptera, Hymenoptera, &c., and especially on the common Geotrupes stercorarius. The leading character of the species, or so-called species, is, that the dorsal surface is not covered by one chitinous plate, but by two separate ones, leaving a soft white space between them and round the hinder plate. (This is shown in Plate XXII. fig. 2.)

Geoffroy† followed Linnæus, calling the creature "mite des coléoptères;" and De Geer‡ also preserved it, calling it "Acarus fucorum." Schrank §, Hermann ||, Frisch ¶, and others of the earlier writers also treat it as a well-established species. It was, however, Latreille ** who instituted the genus Gamasus; and he made coleoptratorum the type of a new genus, Carpais, which genus he abandoned †† in his later works. The creature, from its abundance, came to be considered as a type of the Gamasinæ, which type has been followed by numerous writers down to the present time. Dr. Kramer in 1876‡‡ points out that more than one species has been included in the name "Gamasus coleoptratorum;" he defines them, and makes the separation of the two dorsal plates a ground for dividing the genus Gamasus into subgenera.

Other writers, such as Koch §§, have made the presence of a space between the two dorsal plates, or the visibility of the line of juncture, a means of classification.

Kramer's paper appeared in the first number of the 'Archiv für Naturgeschichte' for 1876; in May of the same year appeared Mégnin's paper above cited (in Robin's 'Journal de l'Anatomie' &c.). Mégnin utterly denies that coleoptratorum is a species at all. He says that the division of the plates on the back simply shows that the creature is in an immature stage, and is a nymph, or, rather, is constituted of the nymphs of at least three species, of

^{*} Syst. Nat. 13th ed. p. 1026. no. 27.

[†] Hist. Ins. tom. ii. p. 623. no. 4.

^{† &#}x27;Mém. pour servir à l'hist. des Insectes' (Stockholm, 1778), tome vii. p. 112.

^{§ &#}x27;Obs. Hist. Nat.' tab. i. fig. 13.

^{| &#}x27;Mémoire aptérologique' (Strasbourg, 1804), p. 74.

[¶] Ins. tom. iv. tab. 10.

^{** &#}x27;Précis des Car. gén. des Ins.' 1796.

^{§§ &#}x27;Uebersicht des Arachnidensystems,' 3tes Heft (Nürnberg, 1842).

which Gamasus crassipes is one; and he abandons the division of the dorsal plate as a means of classification.

In 1879* Kramer replied, and affirmed that some of the adult Gamasinæ do show divisions between the dorsal plates, and adhered to it as a mode of distinction; he states that he has seen ripe eggs inside a species which he calls *G. nemorensis*, and which had divided plates on the back.

Linnæus † also named another well-known species, his Acarus (now Gamasus) crassipes. There has been a good deal of confusion with this species—Schrank and others having called allied species crassipes simply because they had the second pair of legs thickened, which is certainly only characteristic of the males, and is common to several species. Hermann, however, although his description is imperfect, gives figures ‡ which sufficiently identify the Linnean species. Hermann also gives a similar species, but without the thickened legs, which he calls Acarus testudinarius; and another, A. marginatus, the characteristic of which is showing a soft white line between the single chitinous dorsal plate and the ventral plate.

Mégnin asserts §:—First that the Gamasus crassipes of Dugès is the adult male of one of the three species of which coleoptratorum is the nymph; but as Dugès does not describe or figure the species, but simply refers to Hermann, this is equivalent to saying that coleoptratorum is the nymph of Hermann's crassipes. Secondly, that testudinarius is the female of crassipes; in this he is followed by Canestrini and Fanzago||. And, thirdly, that the characteristic of marginatus is simply that of the females of a large portion of the genus.

It was to assist in settling these various points and to learn what else I could of the life-histories of these creatures that I undertook the following observations, chiefly on crassipes and coleoptratorum. Whatever may be their value, they are, to the best of my ability, in every instance, faithful records of what I have actually seen take place with selected and known specimens in cages which I could place upon the stage of my microscope for frequent watching.

^{* &}quot;Ueber einige Unterschiede erwachsener und junger Gamasiden," Archiv für Naturgeschichte, 1879.

[†] Syst. Nat. ed. 12, sp. 8; Faun. Suec. 1769.

[‡] Loc. cit. pl. 3. fig. 6, and pl. 9. Q, R. § Loc. cit. p. 330.

[&]quot;Intorno agli acari italiani," Atti del. R. Ist. Venet. di Sci. 1877-78.

Observations on Gamasus coleoptratorum.

First Generation.—On the 14th April, 1880, I captured, amongst some rubbish in my own garden, two Gamasinæ which, in my opinion, decidedly belonged to one of the species known as coleoptratorum, with the strongly divided dorsal plate, although they were not at the moment parasitic on the beetle. One is figured on Plate XXII. fig. 2.

By the 16th April they had become accustomed to the cell, and

did not try to escape.

Up to 25th April they went on without any marked change, other than growing larger, the chitinous plates on the back not increasing in size, but the white margin becoming gradually broader.

On the 26th April I could not find them for a long time; at last I saw their front tactile legs waving about from beneath a dried seed-husk.

On the 27th, not seeing them, I turned the husk over and saw a cast skin; one soon ran out, it was larger, soft, and light coloured, and had evidently just cast the skin. A short time after the second emerged, which also had cast the skin. One, which turned out to be an adult male, was smaller than the other, and eventually became darker; this one is figured (Plate XXIII. fig. 1). Neither of these adults had any division whatever of the dorsal plate; they never became hard, but were of a more leathery texture; they were not Hermann's crassipes, nor had they any resemblance to it.

These two specimens were kept together; and on the 7th of May there were eggs in the cell, and the female continued to lay eggs; these eggs were placed in a separate cell.

19th May, the cell became too dry; the male was dead, but I revived the female with moisture.

Second Generation.—I cannot say when the first (six-footed) larva emerged from one of the above-named eggs: they are small and difficult to see; but they continued to hatch out until the 15th May. These larva were quite white and transparent, and did not show any sign of dorsal plates; they had a singular long hair in the centre of the posterior margin not found in the nymphs or adults. The larva is figured (Plate XXII. fig. 1).

In about three days the larva underwent the first change to the eight-footed asexual nymph; this also was quite white, and did not show any sign of dorsal plates.

After the first nymphal change of skin, the specimens showed the strongly divided dorsal plates, and were in every respect similar to the first pair when originally captured.

On 27th May the first adults appeared; they were of course precisely like those they were bred from, did not show any division of the dorsal plate, and never became hard and chitinous, but remained of a leathery texture.

Third Generation.—The adults bred on the 27th May again laid eggs, and I bred them through a third generation with similar results, which, therefore, I do not detail.

It now remained to show for certain that these actually were the same species as that parasitic upon the beetle; I therefore, on 18th July, 1880, captured a beetle (Geotrupes stercorarius) with a large number of coleoptratorum upon it. The closest examination did not show any difference between these and those bred before. I removed them from the beetle and established them in several cells. They throve just as well as those captured in the open, an interesting circumstance, because Dugès * says, with reference to them: - "It is to be noticed that almost all Gamasids dry up and die in a few hours after being separated from the insect or stone unless they are kept in a damp vase;" and Andrew Murray† repeats this as "a peculiarity of all these parasites on insects." The real fact is that they thrive on precisely the same treatment as those not captured on insects or under stones, and do not require as much moisture as many other non-parasitic Acari, as, for instance, some of the Oribatidæ, which never are parasitic in any stages. Probably Dugès did not supply them with proper food.

From the 1st to the 5th August most of those captured on the beetle became adult.

On 5th August I put an adult male and female of this lot into a small cell together.

On the 9th there was an egg in this cell, which I removed and put in a cell by itself.

On the 11th this egg hatched, and produced a hexapod larva.

On the 14th this larva changed into the nymphal stage.

On the 19th it underwent ecdysis and became a mature nymph;

^{*} Loc. cit. p. 26.

^{† &#}x27;Economic Entomology,' p. 158.

it subsequently became adult, but I am not certain of the day of the change.

I had other eggs which were laid by the same pair of Gamasids, and which I bred through all the changes with a merely confirmatory result.

There were, however, two or three of the nymphs, originally captured on the beetle, which, although they attained the mature nymphal stage, never seemed to get any further. I kept them alive for about three months; they then died without becoming adult.

In all stages the specimens captured on the beetle were precisely like those captured in the open.

A microscopical examination of the cast nymphal skins of this species shows that the dorsal plates are composed of cells, the form and arrangement of which is delineated in Plate XXIII, fig. 8, and which exhibit but little granulation. It will be seen that the cellulation is very different from that of crassipes shown in Plate XXIII. fig. 7; but the cellulation of the ventral plates in the coleoptratorum nymph is very similar to that of the dorsal surface of crassipes.

Observations on Gamasus crassipes.

On the 14th April, 1880, two females and one male of this species were put in a cell by themselves.

On the 21st I noticed eggs in the cell; one of the females seemed to keep possession of a sort of retreat in the moss which had several eggs attached to it.

The egg is an oval with very blunt rounded ends, the surface slightly roughened by irregular depressed lines; it is white, very opaque, and always attached by a few threads to the substance it is deposited on.

The major axis is about '4 millim.

The width at the larger end about '28 millim.

"", smaller", '24 millim.

On the 23rd the first hexapod larva emerged. I put it in a cell by itself with one of the eggs. This larva is drawn in Plate XXII. fig. 3. Like all larvæ of Gamasinæ, it is white and semitransparent.

On the 26th the larva changed to the nymphal state.

This nymph was quite white at first, but gradually became larger and a little darker.

On the 2nd of May the nymph changed its skin. The cast skin did not show any trace of plates, and was quite white, except that there were a few chitinous dots or cells scattered about it, each having a darker nucleus. A few of these cells had approached certain others in little groups, where they had begun to assume a hexagonal or pentagonal form: these cells could not be distinguished on the living creature, but only by examining the cast skin.

The nymph, after the change of skin, did not then show any trace of detached dorsal plates. It continued to get larger and darker up to 15th May, but still did not show dorsal plates.

On 15th May the nymph again changed its skin, and became a perfect male; it was, as usual, rather light at first, but gradually acquired the full hardness and darkness of the adult species, which is wholly dark and chitinous.

Although the nymph up to the last did not exhibit any dorsal plate, yet on examining the cast skin two dorsal plates were clearly visible with a space between them; they were, however, so much lighter and thinner than in *Gamasus coleoptratorum*, that when on the creature they could not be distinguished as plates at all, but only as a slight darkening of the surface. The cellulation was quite different from that of the dorsal plates of *G. coleoptratorum*, being composed of more equal-sided hexagonal or pentagonal cells irregularly placed, and each cell appearing to be formed of smaller granules.

I bred several other specimens, the times being nearly identical from the hatching of the eggs. All the eggs first laid, and which I knew, because I removed them and placed them in separate cells, turned out to be males, all the later laid eggs turned out females. The times occupied by the changes from hatching to attaining the adult form were about the same in the females as the males, and there was the same apparent absence of dorsal plates.

I did not get any perfect females until about a month after the first males had emerged; but of course it is highly probable that, under natural conditions, more eggs might have hatched and a larger proportion been reared; and thus the females might have followed more closely on the males.

These females had the single dorsal plate detached from the sternal plate, and showing the white membranous line between, which was taken by the earlier writers as the characteristic of the so-called species G. marginatus; this line was so narrow at first, that it could scarcely be seen; but as the eggs ripened in the ovary, the abdomen became distended and the line became gradually broader, particularly near the posterior margin, where the large ripe egg (for one only is usually ripe at a time) generally lies.

I bred from these males and females, and traced them through a second generation with similar results.

A point which struck me as singular, and contrary to what has been believed, was the absence of any inert stage before the changes of skin, or from one stage to another. In the Oribatidæ and other Acarina which I have previously watched, each change is preceded by a period of such absolute quiescence that any person not acquainted with the creature would suppose it to be dead; not a sign of life is to be obtained by touching it or otherwise. Mégnin, following Claparède's observations, is of opinion that during this period the whole internal parts dissolve and reform; and he expressly says that this is the case with the Gamasinæ*. I am not able to agree with him in this; for certainly in no specimen which I have bred have I been able to observe any inert period; the creature has only become rather less active for a few hours; and among the thousands of Gamasids which I have had from time to time I never noticed an inert specimen, although one is constantly finding inert Oribatidæ.

Another somewhat important matter in which I do not find myself able to arrive at the same conclusion as Mégnin is the period of copulation. Mégnin was, I believe, the first to point out that in the Dermaleichi (Analges) the adult male copulates, not with the finally adult female, which possesses the strongly marked external vulva, but with the female in an earlier stage, which he calls nubile female (femelle accouplée), at which period it closely resembles the nymph, and does not possess any external vulva. Mégnin points out that copulation takes place by the anus; and there cannot, I think, be any doubt that, with regard to the Dermaleichi, he is right in both respects, subject to the possible dispute as to whether his nubile female is actually distinct from the nymph; he gives very good reasons for thinking that it is. Mégnin, however, does not stop here; he distinctly asserts in his subsequent writings that these two points hold good,

^{*} Loc. cit. p. 323.

not only with the Dermaleichi, but also with all other families of Acarina; and in his treatise on the Gamasinæ before quoted he says (at p. 322):—"Copulation in the Gamasinæ, as in all Acarina which we have observed, does not take place by the vulva of oviposition, which does not exist at the time of copulation, but by the anus. It is not the large, adult, egg-bearing female which receives the male, but the young female, still bearing the appearance of a nymph, and not presenting any trace of sexual organs. It is only after fecundation, and after a final change of skin, that the oviscapte, or vulva of deposition, appears."

I have elsewhere given my reasons for being decidedly of opinion that in the genus Glyciphagus, at all events, copulation takes place with the adult female; and I have now to add that the result of my observations on the Gamasinæ leads me to the conclusion that in those species which I have bred copulation has taken place with the adult female, and not with the female in any immature stage; and, in my opinion, Mégnin is not correct in saying that in the Gamasinæ it takes place by the anus.

I was desirous of seeing how the copulation took place, and particularly how the enlarged second pair of legs of the male in such species as crassipes were used. When my captives got accustomed to the cells, I had several opportunities of watching The adult male rushed up to the adult female (never, in any instance that I saw, to an immature one), approaching her from behind; on reaching her, he turned suddenly over on his back and slipped underneath the female, seized one of her hind legs with each of his enlarged legs of the second pair, which was doubled back upon itself. The leg of the female was clasped between the great apophysis on the second joint of the enlarged leg of the male, which curves forward and upward, and the smaller one on the fourth joint, which in this position of the leg curves backward and downward; this arrangement brings the genital aperture of the male immediately below the vulva of the female, which is placed further back than the male organ. The two are so firmly locked, that they may sometimes be rolled over and examined without separating.

Conclusions.

The principal results of my observations may, in my opinion, be shortly summarized as follows:—

1. That Mégnin is correct in saying that Gamasus coleoptraorum, and other allied creatures with the conspicuously divided dorsal plates, are not species at all, but are immature stages of other species.

- 2. That the division of the dorsal plate is, in most cases at all events, a question of degree, and does not form a sound basis for classification, as applied by Koch, Kramer, and others.
- 3. That the dorsal plates do not grow gradually, but alter in size, shape, or development at the ecdysis.
- 4. That Mégnin is right in saying that the characteristic of the so-called G. marginatus is simply a provision possessed by the females of a large number of species.
- 5. That the extent of the white margin depends upon the extent to which the abdomen is distended by eggs.
- 6. That Mégnin is in error in saying that coleoptratorum is the nymph of crassipes. The nymph of crassipes does not show any divided dorsal plates which can be seen on the living creature.
- 7. That in the species which I have bred there is not any inert stage before the transformations or ecdyses.
- 8. That in the same species copulation takes place with the adult female, and not with the immature one as Mégnin contends, and that it is by the vulva, not the anus.

EXPLANATION OF THE PLATES.

PLATE XXII.

- Fig. 1. Larva of Gamasus coleoptratorum, × about 35.
 - 2. Nymph of Gamasus coleoptratorum, × about 35. It is from this nymph that the so-called species was named.
 - 3. Larva of Gamasus crassipes, × about 35.

PLATE XXIII.

- Fig. 1. Adult male Gamasus coleoptratorum, × about 35.
 - 2. Caruncle and claws of same.
 - 3. Side view of mandible of adult female of same, \times 55, rendered transparent so as to show the articulation of the movable joint, the thickness of the chitine, &c.
 - 4. Organ (qy. tactile?) depending from epistome of Gamasus crassipes.
 - 5. Scattered nucleated chitinous cells on the first nymphal cast skin of Gamasus crassipes.
 - Next stage. Cells aggregating into groups, but still preserving a somewhat rounded outline.
 - 7. Later stage. Cellulation of semitransparent dorsal shield, visible only on the cast nymphal skin: Gamasus crassipes.
 - 8. Cellulation of conspicuous dorsal shield of nymph of Gamasus colenptratorum,

1-2 Larvas Nympu, GAMASUS COLEOPIRATORUM, & Larvas, G.CKASSIPIS.

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